

OBSERVATIONS OF CHROMOSOMES IN *LUDWIGIA* (ONAGRACEAE)¹

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ABSTRACT

Chromosome numbers are reported for 38 of the 45 species of *Ludwigia* (Onagraceae) exclusive of sect. *Myrtocarpus* s. lat., based on a review of the literature and the study of 302 individuals from 283 naturally occurring populations from throughout the range of the genus. The basic chromosome number of the genus is $x = 8$, with no aneuploidy but extensive polyploidy. Among the 38 species of *Ludwigia* exclusive of sect. *Myrtocarpus* s. lat. that have been examined cytologically, there are 14 diploids ($n = 8$), 8 tetraploids ($n = 16$), 6 hexaploids ($n = 24$), 1 octoploid ($n = 32$), and 1 dodecaploid ($n = 48$), together with 4 species that include both tetraploids and hexaploids, 1 that includes both diploids and tetraploids, 1 that includes hexaploids and octoploids, and 1 that includes octoploids and decaploids. In the first two groups of species with intraspecific polyploidy, we believe that the tetraploids have given rise directly by the functioning of unreduced gametes to the populations with higher chromosome numbers. Multivalents have been observed in the genus only in single plants of tetraploid individuals of *L. octovalvis* and *L. pilosa*, and in *L. uruguayensis* ($n = 24, 40, 48$). There is no general correlation between breeding system and level of polyploidy in *Ludwigia*, as is manifest in several genera of annual Onagreae. *Ludwigia* seems less closely related to all other genera of Onagraceae than they are to one another. It originated at least 50 m.y. ago, probably in South America, where the family also is believed to have originated, but it reached the Northern Hemisphere also in the Eocene. The distinctive chromosome morphology of *Ludwigia*, in which the interphase nuclei are dotted with small chromocenters and the distal segments of the chromosomes are diffuse at mitotic mid-prophase, resembles that of Epilobieae, but seems clearly to have originated independently, like the other convergent morphological and physiological features in these two genera, from ancestors with more generalized chromosomes similar to those in *Fuchsia*, *Circaea*, and some species of *Lopezia*. Once the genome $x = 8$ had originated in the common ancestor of *Ludwigia*, polyploidy has been very frequent (at least two-thirds of the species are polyploid), and the genus has attained a very widespread distribution, particularly in the tropics and temperate North America, in the moist habitats where it occurs.

Ludwigia, a pantropical genus that is also well represented in temperate North America and has three endemic taxa in temperate Asia, includes some 80 species and is one of the largest genera of Onagraceae. It is very distinctive within this family and is the only genus of the tribe Jussiaeae. Until the 1960s, the genera *Jussiaea* and *Oocarpon*, and sometimes also the genera *Isnardia* and *Ludwigiantha*, were conventionally segregated from *Ludwigia*, but more recent research and a better understanding of the phylogenetic relationships within the group has led to their grouping together within the genus *Ludwigia* (summary in Raven, 1963a), an alignment that now seems to have been adopted universally.

The chromosomes of *Ludwigia* sect. *Myrtocarpus* s. lat. will be treated by T. P. Ramamoorthy in his forthcoming revision of that group (Ramamoorthy, in prep.). Chromosome counts have been reported earlier for 6 species of sect. *Myrtocarpus* s. lat. out of a total of 32 (Gregory & Klein, 1960; Kurabayashi et al., 1962). In the

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remaining 16 sections of the genus (Raven, 1963a), there are some 45 species, of which chromosome numbers have been reported for what we regard as 16 species. In this paper we are reporting observations on 302 additional individuals representing a total of 283 populations of 38 species, including additional counts of all 16 species reported earlier (Tables 1–2). Of the seven remaining species, for which no chromosomal information is available, one is North American, two are Cuban endemics, and the remaining four are mainly South American, including the one uncounted section, sect. *Oocarpon*. We have also included all earlier reports in this paper with references, amounting to about 30 counts. Unless otherwise indicated, voucher specimens have been deposited at the Missouri Botanical Garden (MO). All counts were somatic except those indicated by “ $n =$ ” numbers in parentheses following the citation of the vouchers. In all cases where the voucher citation is marked with an asterisk, the chromosome number determination was made in progeny grown from that collection, or from plants collected in the wild at the same time and grown on in the greenhouse. All collections prefixed by “R” were made by Raven, and all collections cited in parentheses are greenhouse vouchers.

The first report known to us of chromosomes in plants of the genus *Ludwigia* was that of Sinotô (1928), who reported $n = 8$ in the course of an investigation of pollen development in the taxon now known as *Ludwigia peploides* subsp. *stipulacea*. Chromosomes of another plant of this genus, of which the identity is not certain (see p. 870) were reported by Sharma & Sarkar (1956). They reported distinct differences in chromosome morphology and size within the genome, and that the size of the individual chromosomes ranged from 1–2.3 μm . In the diploid plant they investigated, they reported that some cells had $2n = 14$ and others $2n = 18$, and that even in cells with the normal chromosome number $2n = 16$, differences in chromosome morphology could be observed. Such numerical differences have not, however, subsequently been found to be characteristic of individuals or populations in the genus, in which differentiation at the diploid level and polyploidy are the characteristic modes of differentiation.

Gregory & Klein (1960) reported chromosome numbers in 6 species of what is now regarded as *Ludwigia* sect. *Myrtocarpus* s. lat., and in what we now consider to be 12 additional species and 1 additional subspecies of the genus. They reported for the first time the widespread occurrence of polyploidy in the genus, but found no chromosomal heterozygosity or other irregularities in the samples they examined. They also mentioned differences in size between the chromosomes of different species. Later, in a study of mitotic chromosomes in Onagraceae, Kurabayashi et al. (1963) reported that the interphase nuclei of *Ludwigia* were dotted with small chromocenters which were more densely pycnotic than those of other Onagraceae, and that the distal segments of the chromosomes were diffuse at mitotic mid-prophase. The chromosomes were clearly heterogeneous with respect to their relative lengths and in the proportions of the proximal and distal regions, and they also differed conspicuously in size at metaphase, as reported earlier by Sharma & Sarkar (1956). Their diffuse distal regions were much more evident than the very short and inconspicuous ones of Epilobieae.

From 1962 onward, chromosome numbers were reported for what we would regard as five of the seven species of *Ludwigia* native to Asia (Chuang et al.,

TABLE 1. Chromosomes in *Ludwigia*, except sect. *Myrtocarpus* s. lat.

Section, Genus, Species	Chromosome Number
Sect. <i>Africana</i>	
<i>L. jussiaeoides</i> Desr.	$n = 32$
<i>L. stenorraphe</i> (Brenan) Hara subsp. <i>stenorraphe</i>	$n = 48$
Sect. <i>Brenania</i>	
<i>L. brenanii</i> Hara	$n = 24$
Sect. <i>Caryophylloidea</i>	
<i>L. perennis</i> L.	$n = 8$
Sect. <i>Cryptosperma</i>	
<i>L. abyssinica</i> A. Rich.	$n = 24$
Sect. <i>Dantia</i>	
<i>L. arcuata</i> Walt.	$n = 16$
<i>L. brevipes</i> (Long) E. H. Eames	$n = 24$
<i>L. palustris</i> (L.) Ell.	$n = 8$
<i>L. repens</i> Forst. (<i>L. natans</i> Ell.; Raven, 1965)	$n = 24$
<i>L. spathulata</i> Torr. & A. Gray	$n = 16$
Sect. <i>Fissendocarpa</i>	
<i>L. hyssopifolia</i> (G. Don) Exell	$n = 8$
Sect. <i>Ludwigia</i>	
<i>L. alternifolia</i> L.	$n = 8$
<i>L. hirtella</i> Raf.	$n = 8$
<i>L. maritima</i> Harper	$n = 8$
<i>L. virgata</i> Michx.	$n = 8$
Sect. <i>Macrocarpon</i>	
<i>L. octovalvis</i> (Jacq.) Raven	$n = 16, 24$
Sect. <i>Microcarpium</i>	
<i>L. alata</i> Ell.	$n = 16, 24$
<i>L. curtisii</i> Chapman	$n = 24, 32$
<i>L. glandulosa</i> Walt.	$n = 16$
<i>L. linearis</i> Walt.	$n = 8$
<i>L. linifolia</i> Poir.	$n = 8$
<i>L. microcarpa</i> Michx.	$n = 8$
<i>L. pilosa</i> Walt.	$n = 16$
<i>L. polycarpa</i> Short & Peter	$n = 16$
<i>L. sphaerocarpa</i> Ell.	$n = 16$
<i>L. suffruticosa</i> Walt.	$n = 16, 24$
Sect. <i>Miquelia</i>	
<i>L. ovalis</i> Miq.	$n = 16$
Sect. <i>Nematopyxis</i>	
<i>L. prostrata</i> Roxb.	$n = 8$
Sect. <i>Nipponia</i>	
<i>L. epilobioides</i> Maxim.	$n = 24$
Sect. <i>Oligospermum</i>	
<i>L. adscendens</i> (L.) Hara subsp. <i>adscendens</i>	$n = 16$
<i>L. adscendens</i> subsp. <i>diffusa</i> (Forsk.) Raven	$n = 16$
<i>L. helminthorrhiza</i> (Mart.) Hara	$n = 8$
<i>L. hookeri</i> (Michx.) Hara	$n = 8$
<i>L. peploides</i> (H.B.K.) Raven subsp. <i>glabrescens</i> (O. Kuntze) Raven	$n = 8, 16$
<i>L. peploides</i> subsp. <i>montevidensis</i> (Spreng.) Raven	$n = 8$
<i>L. peploides</i> subsp. <i>peploides</i>	$n = 8$

TABLE 1. Continued.

Section, Genus, Species	Chromosome Number
<i>L. peploides</i> subsp. <i>stipulacea</i> (Ohwi) Raven	$n = 8$
<i>L. uruguayensis</i> (Camb.) Hara	$n = 24, 40, 48$
Sect. <i>Prieurea</i>	
<i>L. senegalensis</i> (DC.) Troch.	$n = 8$
Sect. <i>Seminuda</i>	
<i>L. affinis</i> (DC.) Hara	$n = 32, 40$
<i>L. africana</i> (Brenan) Hara	$n = 24$
<i>L. leptocarpa</i> (Nutt.) Hara	$n = 16, 24$

1962; Sharma & Sharma, 1966; Mitra & Datta, 1967; Baquar, 1968; Pillay, 1970; Shetty & Subramanyam, 1971; Subramanyam, 1971; Sarkar et al., 1973), and the chromosome number for a sixth, *L. epilobioides*, was mentioned by Raven (1963a).

DISCUSSION OF RESULTS

SECT. *AFRICANA*

This ditypic African section consists of one monomorphic species, *Ludwigia jussiaeoides* ($n = 32$), and one extremely polymorphic one, *L. stenorraphe*, in which subsp. *stenorraphe* has $n = 48$. Chromosome counts of the other three subspecies of the latter would be highly desirable, and will probably suggest the taxonomic subdivision of this entity at the specific level (cf. Raven, 1963a).

SECT. *BRENANIA*

A very distinctive and local autogamous species, the hexaploid *Ludwigia brenanii* is known only from the Volta River drainage in southeastern Ghana.

SECT. *CARYOPHYLLOIDEA*

The diploid *Ludwigia perennis* is widespread in the Old World, highly autogamous, and morphologically quite uniform. The report by Pillay (1970) of $n = 16$ in this species may have been based on material of another species and needs to be confirmed. The material we counted from the same locality (Imphal) had $n = 8$ like all other populations of the species we have examined.

SECT. *CRYPTOSPERMA*

This monotypic section consists solely of the widespread, uniform, autogamous African endemic, *Ludwigia abyssinica*, which is hexaploid. As far as known, it is entirely hexaploid and has no close relatives.

SECT. *DANTIA*

This section will be treated in more detail by Schmidt & Raven (in prep.). Of the seven species listed by Raven (1963a), *Ludwigia* × *lacustris* E. H. Eames

is a sterile triploid hybrid, and *L. verticillata* Munz is a synonym of *L. inclinata* (L.f.) Raven (sect. *Myrtocarpus* s. lat.), a species in which the leaves on the lower, prostrate stems are verticillate, those on the upper flowering branches spirally arranged. Plants of *L. inclinata* in which the episepalous stamens are lacking occur intermixed with others in which they are present in the same populations, at least locally.

Of the remaining five species properly assigned to sect. *Dantia*, one is diploid, two are tetraploid, and two are hexaploid. All are autogamous except *L. arcuata*, in which the stigma is elevated above the anthers at anthesis (Schmidt, 1967).

SECT. *FISSENDOCARPA*

A morphologically uniform and widespread autogamous tropical weed without any close relatives, *Ludwigia hyssopifolia* is likewise apparently quite uniform cytologically, and entirely diploid.

SECT. *LUDWIGIA*

This section comprises four closely related and more or less interfertile species of which three are confined to the southeastern United States, and the fourth extends north to the midwestern states and southernmost Canada. All are diploid. Only *Ludwigia virgata* is regularly outcrossing, and in that species, the stigma is elevated well above the anthers at anthesis.

SECT. *MACROCARPON*

All species of sect. *Macrocarpon* except the widespread, weedy, autogamous *Ludwigia octovalvis*, long known as *Jussiaea suffruticosa* L., are restricted to the New World. They are being studied in detail, and their chromosome numbers will not be reported here, except to mention that among them are diploid species and two that are genetically self-incompatible.

Within *Ludwigia octovalvis* there are striking morphological differences that are reflected in a complex synonymy and in earlier efforts to divide the species into subspecies (Raven, 1963a). The kinds of densely pubescent, robust plants that we referred earlier to *L. octovalvis* subsp. *sessiliflora* (Mich.) Raven are especially distinctive in their extreme form, but they often grow side-by-side with less densely pubescent, more slender plants, the differences maintained by autogamy. In South America and Africa, the two sorts are nearly exclusively tetraploid ($n = 16$), whereas in Asia, the kinds of plants that exhibit parallel patterns of variation are almost all hexaploid ($n = 24$). To attempt to recognize the differences between these two sorts of plants in the formal taxonomy does not seem to accord with the biological realities of a remarkably complex species, and we now agree with Sreemadhavan (1966) that the species should not be subdivided formally (Raven, 1977).

The most distinctive race within the species, both morphologically and geographically, is that designated earlier as *Ludwigia octovalvis* subsp. *brevisepala* (Brenan) Raven (Raven, 1963a). Plants of this sort are abundant over most of Africa, where they are usually the only type of the species represented. In Mad-

agascar, southern and southeastern subtropical Africa, however, plants of the “*sessiliflora*-type,” tetraploid like similar plants which are common in Brazil and elsewhere in South America, appear. Between the area occupied by such plants and the large, tropical African area of “*brevisepala*,” plants like those characteristic of “*subsp. octovalvis*” in the rest of the world—i.e., relatively robust, large flowered, and less pubescent than “*sessiliflora*”—are frequent. It is possible, as suggested earlier, that the “*octovalvis*-type” plants in Africa might have originated following hybridization between “*brevisepala*-type” and “*sessiliflora*-type” plants; but autogamy is certainly the rule in all populations of this species worldwide. Taxonomically, it would be possible to continue to recognize “*brevisepala*-type” plants as a distinctive African subspecies, but to do so would be to leave a bewildering diversity of much more variable plants, widespread throughout the rest of the tropics and subtropics, grouped as *subsp. octovalvis*, since we are convinced that there is no practical way to continue to separate *subsp. sessiliflora* as a useful taxonomic entity.

With respect to chromosome number, most of the populations in the New World and all of those, as far as known, in Africa, are tetraploid ($n = 16$). The majority of populations in Asia, occupying an area extending to New Guinea and northern Australia, are hexaploid ($n = 24$). Plants from the Pacific Islands eastward to the New Hebrides and New Caledonia, in contrast, are tetraploid. Tetraploids also seem to occur locally in Asia, at least near Calcutta, India (Subramanyam, 1971; Sarkar et al., 1973) and near Chiangmai, Thailand. Reports of $n = 8$ and $2n = 16$ in this species from India (Mitra & Datta, 1967: 458, withdrawn by N. Datta in litt.; Sheriff & Mahalakshami, 1969, from Bangalore) seem to have resulted from confusion with other species, since later chromosome counts of other populations from the same areas have uniformly been $n = 24$. *Ludwigia octovalvis* is a very frequent weed of moist cultivated areas, readily carried about by commerce, and it seems to occur everywhere in the Pacific where there is human activity. The cytological pattern outlined here suggests that tetraploids from the New World have colonized both Africa and the islands of the Pacific, perhaps at least several times each, and that the widespread hexaploids of tropical Asia have originated there.

The two populations of *Ludwigia octovalvis* from the New World that had a gametic chromosome number of $n = 24$, one each from the Dominican Republic and from Venezuela, seem to be isolated cases. Hexaploid individuals in this species can doubtlessly arise directly from the tetraploids, as described earlier for *Gaura coccinea* Pursh (Raven & Gregory, 1972), and perhaps the hexaploids encountered represented only single populations, or even single individuals, that had originated in this way. This situation will be investigated further.

Of particular interest is the tetraploid individual from Clay Co., Florida, mentioned above. At meiotic metaphase I, it had 12 bivalents and 2 rings of 4 chromosomes, thus being one of the very few plants of *Ludwigia* in which meiotic irregularities have been found in a natural population.

Finally, it should be noted that populations of diploid ($n = 8$) individuals similar to *L. octovalvis* are frequent in Mexico, although they have not been found within the United States thus far. Examples of populations with $n = 8$ are as follows:

MEXICO. BAJA CALIFORNIA: Cape Region, *Thomas 7699**. GUERRERO: *Graham 427** (DS; R67-L47). JALISCO: *McVaugh 1659** (MICH; R62054). MICHOACÁN: *Porter 1391** (DS); ca. 17 mi E of Morelia, *Breedlove 7228* ($n = 8$).

Diploid populations of this sort can be distinguished only with difficulty from tetraploid populations of *Ludwigia octovalvis*, but they do have larger flowers and may well merit specific recognition. By Munz (1942) they were treated as *Jussiaea bonariensis* Mich. [= *L. bonariensis* (Mich.) Hara] when they were recognized as distinct from *J. suffruticosa* L. (= *L. octovalvis*), but they do not seem to be equivalent to the southern South American populations that include the type of that species. The much larger-flowered plants naturalized at Wilmington, New Hanover Co., North Carolina, on the other hand, are very distinct from any Mexican populations and may be the same as the South American ones, and have $n = 16$ (R18731). At any event, the Mexican diploid plants that resemble *L. octovalvis* must closely resemble the ancestral populations of this species, which might have originated essentially as an autotetraploid, with subsequent selection against quadrivalent formation. In any event, it is highly likely that the rings of chromosomes observed in the tetraploid Florida population of *L. octovalvis* mentioned above may reflect intergenomic chromosomal homology, and not the presence of reciprocal translocations within this plant.

SECT. *MICROCARPIUM*

Ludwigia sect. *Microcarpium* is a diverse but distinctive polyploid complex centering in the southeastern United States and extending into the islands of the Caribbean. Chromosome counts are now available for all taxa except the distinctive Cuban endemic *L. stricta* Wright ex Sauvalle, and, if it is distinct from *L. alata*, *L. lanceolata* Ell. The remaining ten species of the section consist of three diploids, *L. linearis*, *L. linifolia*, and *L. microcarpa*; four tetraploids, *L. glandulosa*, *L. polycarpa*, *L. pilosa*, and *L. sphaerocarpa*, of which the latter two are very closely related and appear to replace one another geographically and to intergrade in nature; and three species that have more than one chromosome number—*L. alata* ($n = 16, 24$); *L. curtisii* ($n = 24, 32$); and *L. suffruticosa* ($n = 16, 24$). In both *L. alata* and *L. suffruticosa*, it is likely that the hexaploids arose directly from the tetraploids by the functioning of an unreduced gamete, as postulated above for populations of *L. octovalvis* (sect. *Macrocarpon*) in the Dominican Republic and in Venezuela. The situation in *L. curtisii* is apparently more complex, with the diploid *L. microcarpa* evidently having played a role in the evolution of the polyploid complex. Within this group, the differentiating characteristics ascribed to *L. spathulifolia* and to *L. simpsonii* certainly are not correlated with the differences in chromosome number and, furthermore, are subject to environmental modification so that capsule shape and size and leaf shape, which may appear distinctive in the field, tend to converge in the experimental garden.

Within the section, *Ludwigia linifolia* ($n = 8$), *L. glandulosa* ($n = 16$), and *L. polycarpa* ($n = 16$) seem related, as do *L. stricta*, *L. microcarpa* ($n = 8$) and *L. curtisii* ($n = 24, 32$); in turn, there might well be a relationship between these two groups. Species in which the apex of the ovary and nectaries are yellow and

attractive to insects, even though the flowers lack petals, are *L. pilosa* ($n = 16$) and *L. sphaerocarpa* ($n = 16$), which as we have mentioned are very closely related and possibly even best regarded as conspecific, and *L. alata* ($n = 16, 24$), *L. lanceolata* (if it is distinct), and *L. suffruticosa* ($n = 16, 24$). There may very well be a relationship between the first two species and the last three, even though the first two shed their pollen in tetrads, the last two singly (Raven, 1963a). Petals occur in species of sect. *Microcarpium* only in *L. linifolia* ($n = 8$), *L. stricta*, and *L. linearis* ($n = 8$); recently Eyde (1978) has shown that the last-mentioned species differs from all others assigned to the section in having the sporogenous tissue in its anthers divided into packets by sterile tissue. Despite this characteristic, it resembles *L. glandulosa* ($n = 16$) morphologically and might be directly related to it. Biosystematic investigations to clarify the relationships of the species of this complex further are underway.

The collection of *Ludwigia pilosa* from Colleton Co., South Carolina, mentioned above, formed 14 bivalents and a ring of 4 chromosomes at meiotic metaphase I. As in the individual of *L. octovalvis* discussed above, it is presumed that the ring of chromosomes was formed because of homology between the two genomes combined in this species, and not because of the presence of a reciprocal translocation, but the situation should be investigated further.

SECT. MIQUELIA

Ludwigia ovalis, a very distinctive East Asian species, combines the prostrate habit of sect. *Dantia*, the spirally arranged leaves of sect. *Microcarpium*, and its own very specialized seeds. It certainly finds its closest relatives in these primarily North American sections of temperate to subtropical regions. As far as known, it is tetraploid.

SECT. NEMATOPYXIS

Ludwigia prostrata is a highly autogamous, diploid species without any close relatives.

SECT. NIPPONIA

As reported earlier (Raven, 1963a), both subspecies of *Ludwigia epilobioides*, an autogamous, distinctive East Asian species, are hexaploid ($n = 24$).

SECT. OLIGOSPERMUM

The chromosome numbers reported here, which include all species of the section except for the Cuban endemic *Ludwigia peduncularis* (Wright ex Gris.) Gómez, indicate that this very widespread group is a polyploid complex. Owing to the complex pattern of intergradation in Madagascar (Raven, 1963a), and to the demonstrated tetraploidy of *L. adscendens* subsp. *adscendens*, we are now tentatively following Raynal (1966) in part in treating the entities we earlier distinguished as *L. stolonifera* and *L. adscendens* as subspecies of an Old World tetraploid species. This species and the New World, white-flowered *L. helmin-*

thorrhiza ($n = 8$) are the only members of the section in which pneumatophores are consistently formed on the floating stems; all members of the group form such pneumatophores from the underground parts. Of the taxa of this section, only *L. helminthorrhiza* and *L. adscendens* subsp. *adscendens* have white petals, instead of the more frequent bright yellow ones.

Contrary to Raynal (1966), we still prefer to maintain the diploid *Ludwigia peploides* as a distinct species, even though it is represented both north and south of the tropical area of *L. adscendens* subsp. *adscendens* in Asia and Australia. An experimental hybrid between the strain of *L. peploides* subsp. *glabrescens* reported above from Arkansas and that of *L. peploides* subsp. *stipulacea* from Kanagawa Prefecture, Japan, which was grown in the greenhouse formed 8 bivalents at meiotic metaphase I and was fully fertile as to both pollen and seed set. Presumably the tetraploid plant of *L. peploides* subsp. *glabrescens* reported above from Mississippi had had a local origin. The chromosome number $2n = 24$ reported by Chuang et al. (1962) for *L. peploides* subsp. *stipulacea* from Taiwan is almost certainly based upon a spontaneously occurring triploid individual with one unreduced gamete, and some of the elements in their drawing resemble trivalents. The chromosome number $n = 8$ is presumably characteristic of this entity in Taiwan as elsewhere in its wide range. More puzzling is the report of Sharma & Sarkar (1956) of a diploid individual of *L. adscendens* subsp. *adscendens* from India, but the report needs to be confirmed. The authors stated that the flowers of the plant they examined were either yellow or white, strongly suggesting that other species, perhaps the diploid *L. perennis*, may have been involved.

Otherwise, it appears that there may be two distinct elements within *Ludwigia uruguayensis*, one with $n = 24$ (and $n = 48$) and the other with $n = 40$. Multivalents are frequent in both, and they might well be separable taxonomically following further study. Based on a single count, *L. hookeri* seems to be diploid, whereas the Cuban *L. peduncularis* is probably a high polyploid, judged from its 5–8-pored pollen.

SECT. *PRIEUREA*

As discussed earlier (Raynal, 1966; Raven, 1978), the segregation of taxonomic units within this vegetatively plastic section appears indefensible in view of the behavior of the plants observed under different conditions in the experimental garden. We therefore regard this section as comprising a single, diploid species. The species forms a number of distinctive biotypes which are presumably reinforced by its almost total autogamy. It has no apparent relatives within the genus.

SECT. *SEMINUDA*

Ludwigia sect. *Seminuda* constitutes a polyploid complex in which no diploids have yet been discovered. Only the New World populations of *L. leptocarpa* are known to be only tetraploid, with all other strains examined hexaploid, octoploid, or decaploid. Whether the patterns implied by the results reported here will hold true awaits further chromosome number determinations, especially within *L. affinis* and the South American and African populations of *L. leptocarpa*.

GENERAL DISCUSSION

Chromosome numbers are now available for 38 of the 45 species of *Ludwigia*, excluding sect. *Myrtocarpus* s. lat., and for 16 of the 17 sections of the genus, including all except the monotypic sect. *Oocarpon*. All 25 species of *Ludwigia* that occur in the Old World have now been studied cytologically. Within the group of 38 species for which chromosome numbers are available, there are 14 diploids ($n = 8$), 8 tetraploids ($n = 16$), 6 hexaploids ($n = 24$), 1 octoploid ($n = 32$), and 1 dodecaploid ($n = 48$), as well as 4 species that include both tetraploids and hexaploids, 1 that includes diploids and tetraploids, 1 that includes hexaploids and octoploids, and 1 that includes octoploids and decaploids. In the first two classes of intraspecific polyploidy, we believe that the tetraploids have given rise to the hexaploids (by the functioning of an unreduced gamete) and octoploids directly. The latter two cases, involving *L. curtisii* and *L. affinis*, require further investigation. Polyploidy is well scattered throughout the different sections, and two—*Africana* and *Seminuda*—seem to be exclusively polyploid.

As reported above, multivalents were observed at meiotic meiosis in single plants of tetraploid individuals of *Ludwigia octovalvis* and *L. pilosa*, and were frequent in plants of *L. uruguayensis* with the three chromosome numbers encountered in that complex species, $n = 24, 40,$ and 48 . We consider all of these multivalents to be associated with intergenomic homology, and there is no unequivocal evidence for the presence of reciprocal translocations in *Ludwigia*, either in naturally occurring plants or in hybrids. No evidence of inversions has been encountered either.

In the 45 species of *Ludwigia* that have not traditionally been included in sect. *Myrtocarpus* s. lat., there appears to be no general correlation between breeding system and polyploidy. Approximately 29 of the species are normally self-pollinating, including representatives of every section except *Africana* (2 species); of the 14 known diploids, 7 are mainly outcrossing. The only modally outcrossing species in sect. *Dantia* is a tetraploid; the 7 species of sect. *Oligospermum* are outcrossing as a group (except perhaps for *L. hookeri*), regardless of the level of polyploidy; and the ditypic African polyploid sect. *Africana* is entirely polyploid and outcrossing. Moreover, there is no apparent correlation between the extent of vegetative reproduction and polyploidy.

In terms of its relationships within the family, *Ludwigia* now seems to represent a distinct branch from the common ancestor of the family, with all other living genera on the other branch (Broekens, 1924; Johansen, 1929; Melchior, 1964; Takhtajan, 1959, 1966; Eyde & Morgan, 1973; Eyde, 1977, 1978, pers. comm.). In cladistic terms it is the "sister group" of all other Onagraceae. This relationship implies that the distinctive chromosomes of *Ludwigia*, which are specialized both in number and in morphology (Kurabayashi et al., 1962), were derived from an ancestor common to *Ludwigia* on the one hand and all other members of the family on the other. From this common ancestor, which almost certainly had a gametic chromosome number of $n = 11$ and generalized chromosomes that did not contract unevenly or remain dotted with obvious chromocenters in interphase like those of *Ludwigia* (Kurabayashi et al., 1962), *Ludwigia*, with $x = 8$ and highly specialized chromosomes, was derived. This event seems almost certainly to have taken place in South America (Skvarla et al., 1978), the

center for the evolution and radiation of *Ludwigia* (Raven, 1967; Raven & Axelrod, 1974). Both the hypothetical common ancestor of the family and the original species of *Ludwigia* seem to have had 4+-mery (Eyde, 1978), whereas 4+-mery evidently was characteristic of the common ancestor of all other Onagraceae, and interxylary phloem clearly originated in the family within this second major line (Carlquist, 1975).

Although diverse enough, particularly in the characteristics of the seeds, capsules, and androecia, to be divided into at least 17 sections (Raven, 1963a), *Ludwigia* is in other respects, such as pollen (Skvarla et al., 1975, 1976), one of the most homogeneous genera of Onagraceae. Its pollen is known from the Eocene of South America (González G., 1967), British Columbia (Rouse, 1962), and the Soviet Far East (Bratseva, 1969), indicating not only a considerable antiquity for the genus, but also an early dispersal to North America and the rest of the world (Raven & Axelrod, 1974). Within *Ludwigia*, the 5(-6)-merous line that includes sect. *Oligospermum* and the closely related sect. *Oocarpon* seems to have diverged from the extinct common ancestor of sect. *Myrtocarpus* s. lat. before the stabilization of 4-mery in the genus (Eyde, 1977). Since the pollen is shed singly in sects. *Oligospermum* and *Oocarpon*, and in tetrads in all other outcrossing species of *Ludwigia*, this also implies that the common ancestor of *Ludwigia* shed its pollen singly, and that the habit of shedding the pollen in tetrads originated separately in *Ludwigia* and in the Epilobieae, as earlier hypothesized (Skvarla et al., 1975). The evolutionary relationships outlined here also suggest that the specialized chromosome morphology of *Ludwigia* and of Epilobieae, which is somewhat similar, and the paludal habit of these two groups, likewise evolved separately. Such a conclusion is in accordance with evidence derived independently from Epilobieae, which suggests that the common ancestor of that tribe, which seems clearly to have originated in the Northern Hemisphere and almost certainly in western North America, occurred in xeric habitats (Raven, 1976). Epilobieae, Onagreae, and Lopezieae, the three tribes in which interxylary phloem occurs (Carlquist, 1975), all seem to have originated in western and southern North America and might conceivably even have a common ancestor with *Fuchsia*, which is mainly South American, and *Circaea*, widespread in temperate forests of the Northern Hemisphere. *Hauya*, which lacks interxylary phloem (Carlquist, 1975), shares some similarities with Onagreae and might represent an offshoot of the line leading to that large and diverse tribe, unless convergent evolution was involved.

Ludwigia, then, has been a successful genus of wet habitats in the tropics for at least 50 million years, with several well-developed temperate offshoots, particularly in North America but also in Asia. Once the chromosome number of this genus stabilized at $n = 8$, there have been no further aneuploid changes, but polyploidy has been frequent and an important part of the evolutionary strategy in most parts of the genus. Unlike the situation in Onagreae, polyploidy in *Ludwigia* does not appear to be correlated closely with autogamy, and, for the present, one can only speculate about the reasons for this major evolutionary difference, which presumably reflects some aspect of the adaptive systems of the two groups. It may be pointed out, however, that the autogamous polyploids of Onagreae are almost invariably annuals, with their presumed emphasis on r -selected

exploitation of highly specific marginal habitats in which the production of a very high frequency of precisely adapted individuals may be at a higher premium than in the wet, and thus perpetually open, habitats of *Ludwigia* species.

TABLE 2. Chromosomes in *Ludwigia*, except sect. *Myrtocarpus* s. lat.

Sect. <i>Africana</i>
<i>Ludwigia jussiaeoides</i> Desr. ($n = 32$).
MOZAMBIQUE. Cabo Delgado Dist., Torre & Paiva 1165* ^a (LISC, R67-L14).
<i>Ludwigia stenorrhapha</i> (Brenan) Hara subsp. <i>stenorrhapha</i> ($n = 48$).
GHANA. S of Attebubu, Morton A465*. TOGO. Nr. Defale, Morton A4426* (MO; R18109).
ZAMBIA. Nr. Chingola, Fanshawe in 1968*; Ndola, Mutimushi 748* (K, R67-L11); 55 km N of Kasempa, Robinson 5547* (K, R67-L12).
Sect. <i>Brenania</i>
<i>Ludwigia brenanii</i> Hara ($n = 24$).
GHANA. Hall 899* (R67-L9); Kete Krachi, Volta R., Hall VBS022* (R19702).
Sect. <i>Caryophylloidea</i>
<i>Ludwigia perennis</i> L. ($n = 8$).
BANGLADESH. Rangamati, Chittagong Hill tracts, Bangladesh, Baquar in 1967 ($n = 8$; Baquar, 1968, as <i>L. parviflora</i>). INDIA. Gauhati, Santapau 35508* (R19094); Bombay, Patel* (R18066, DS); Imphal, Manipur, progeny, R17440; Hooghly, Kamarkundu, West Bengal, India, Shetty 82 ($n = 8$; Shetty & Subramanyam, 1971). PHILIPPINES. Mt. Makiling and vicinity, Laguna Prov., Stern 2340 ($n = 8$). ZAMBIA. Mazubuka Dist., van Rensburg 1907 (SRGH, R32).
Sect. <i>Cryptosperma</i>
<i>Ludwigia abyssinica</i> A. Rich. ($n = 24$).
ETHIOPIA. Wallaga Prov., Mooney 6793* (S, R61-3; also $n = 24$). NIGERIA. Ibadan, Oyo Prov., Morton in 1961* (R17122, R18067). SIERRA LEONE. Nr. Fintonia, Morton & Gledhill S1486*. ZAÏRE. Nr. Kinzaou Vuete, Compère 256* (BR, R61-13).
Sect. <i>Dantia</i>
<i>Ludwigia arcuata</i> Walt. ($n = 16$).
UNITED STATES. Florida: Hillsborough Co., Tampa, Lakela 24805* (also $n = 16$); nr. Tallahassee, Leon Co., Godfrey 62861*; 2 mi S of Oakland, Orange Co., Godfrey 57332* (RSA; $n = 16$, Gregory & Klein, 1960).
<i>Ludwigia brevipes</i> (Long) E. H. Eames ($n = 24$).
UNITED STATES. North Carolina: Byrds Mill Pond, S of Bunnlevel, Harnett Co., Ornduff 6465* (R18101, also $n = 24$); Holts Lake, 4 mi SW of Smithfield, Johnston Co., Ornduff 6463* (R18104, also $n = 24$); 3.2 mi N of Lumberton, Robeson Co., Lloyd 1030* (also $n = 24$).
<i>Ludwigia palustris</i> (L.) Ell. ($n = 8$)
COSTA RICA. Tres Ríos, Cartago Prov., R in 1967*. FRANCE. Sologne, Schotsman (P; Schotsman, 1970). PORTUGAL. Santana Ferreira, Matas de Foja, Queirós 1720, 6038 (COI; Queirós, 1976). UNITED KINGDOM. Hatchet Pond, near Beaulieu, Hampshire, England, R16321 ($n = 8$). UNITED STATES. Arkansas: Terre Noir Creek bottoms, Clark Co., Demaree 48955*; 10 mi W of Hot Springs, Garland Co., Munz & Gregory 23502 (RSA; Gregory & Klein, 1960, as var. <i>americana</i>). California: Santa Cruz Co., V. Hesse in 1961* (R17943, 17944; $n = 8$); Sonoma Co., Rubtzoff 4778* (R18068; $n = 8$). North Carolina: 8 mi N of Fayetteville, Cumberland Co., Lloyd 1025*. 5.1 mi S of Lillington, Harnett Co., Lloyd 1021*. 3.2 mi N of Lumberton, Robeson Co., Lloyd 1029*. Oklahoma: Adair Co., R20420*. Texas: 12 mi W of Beaumont, Jefferson Co., Munz & Gregory 23459 (RSA; $n = 8$; as var. <i>nana</i>); Liberty Co., R19649*, 19650*. Virginia: Lloyd* (R18089); Isle of Wight Co., Lloyd 712* ($n = 8$).
<i>Ludwigia repens</i> Forst. (<i>L. natans</i> Ell.; Raven, 1965) ($n = 24$).
MEXICO. Nuevo León: Río Ramos, between Monterrey and Linares, Hotchkiss & Tindale* (R19634). UNITED STATES. California: San Bernardino Co., R16681 ($n = 24$). Florida: 37 mi SE of Perry, Dixie Co., Munz & Gregory 23467 (RSA; $n = 24$; as <i>L. natans</i> var. <i>natans</i>); Orange Co., Lakela 24902* (R17933, $n = 24$), 24903 in part* (R17932). Texas: Fort Bend Co., R19402 ($n = 24$).

TABLE 2. Continued.

Ludwigia spathulata Torr. & A. Gray ($n = 16$).

UNITED STATES. Florida: Ca. 2 mi N of Woodville, Leon Co., *Godfrey 62880** (DS, FSU, NY; also $n = 16$).

Sect. *Fissendocarpa*

Ludwigia hyssopifolia (G. Don) Exell ($n = 8$).

BORNEO. Kuching, *Hsuan Keng** (R65-69). BRAZIL. Santana, Terr. Amapa, *Pires et al. 51108** (R20185). CHINA. Sah-Pai, Taipeh Co., Taiwan, *Chuang et al. 4321** ($n = 8$, R18065). INDIA. Bombay, *Patel** ($n = 8$, R18066); Cuttack, 300 mi N of Waltair, *P. N. Rao** (R20188); Bangalore, *Satyannarayanachar** (R74-149); Hooghly, Kamarkundu, W. Bengal, *Shetty 86* ($n = 8$; Shetty & Subramanyam, 1971). NEPAL. Ghorwa, ca. 300 m elev., below Ilam, *Hara & Kurosawa in 1963**. PERU. Dept. Loreto, *Mathias 3496** (RSA, R62034); Prov. Quispicanchis, *Vargas 15356** (US). PHILIPPINES. Davao City, *Pancho in 1963** (RG65-68); Mt. Makeling and vicinity, *Stern 2217* ($n = 8$; MO). EL SALVADOR. Dept. San Salvador, *Porter 1289** (GH, RG65-26). SAMOA. Apia, *Carlquist** (RG65-67). SIERRA LEONE. *Morton SL1219**. SURINAM. 20 km N of airstrip, Kabalebo R., *Florschütz & Maas 2562* (U; Gadella & Kliphuis, 1968). ZAÏRE. *Wagemans 2299** ($n = 8$; BR).

Sect. *Ludwigia*

Ludwigia alternifolia L. ($n = 8$).

UNITED STATES. Arkansas: Garland Co., *Demaree 40523* ($n = 8$, Gregory & Klein, 1960, as var. *pubescens*). Florida: Jefferson Co., *R18615* ($n = 8$). Georgia: Jasper Co., *R18706**; Meriwether Co., *R18559* ($n = 8$). Iowa: Johnson Co., *P. Sorensen in 1961** (R20231). Kansas: Reno Co., *Anderson 2811** (DS; R20229). Massachusetts: Middlesex Co., *Solbrig** (R20237). Mississippi: Jackson Co., *R18584* ($n = 8$); Lauderdale Co., *R18565* ($n = 8$); Perry Co., *R18574* ($n = 8$). North Carolina: Orange Co., *Totten** (R20227, R20232); Sampson Co., *Lloyd 1117* ($n = 8$). Rhode Island: Washington Co., *R16517* ($n = 8$). South Carolina: Beaufort Co., *Gregory 533* ($n = 8$); Oconee Co., *Ornduff in 1962** (R18053).

Ludwigia hirtella Raf. ($n = 8$).

UNITED STATES. Florida: Baker Co., *R18695* ($n = 8$). Georgia: Colquitt Co., *Godfrey 67460**; Grady Co., *Godfrey 63223**.

Ludwigia maritima Harper ($n = 8$).

UNITED STATES. Alabama: Baldwin Co., *R18589**. Florida: Jefferson Co. *R18614* ($n = 8$); Nassau Co., *R18700**; Orange Co., *Godfrey 57354** ($n = 8$; RSA, Gregory & Klein, 1960).

Ludwigia virgata Michx. ($n = 8$).

UNITED STATES. Florida: Baker Co., *R19654**; Wakulla Co., *R18606* ($n = 8$). Georgia: Grady Co., *Godfrey 63222** (R19728). North Carolina: New Hanover Co., *Ahles** (R65-41).

Sect. *Macrocarpon*

Ludwigia octovalvis (Jacq.) Raven. Plants with $n = 16$.

BRAZIL. Santana, Terr. Amapá, *Pires et al. 51109**; Itajai, Est. Santa Catarina, *Sehnem** ($n = 8$; R18097); *Dietrich** (R74-174); Est. São Paulo, *Ormond 121** (R67-L6), *128** (R67-L4). COSTA RICA. Prov. Puntarenas, *R21982* ($n = 16$), *Sullivan 382** (DS, R67-L46); Prov. Cartago, *Dressler in 1965** (R65-183). DOMINICA. *Ernst 1328** (DS; R67-L16). FIJI. *Parham 14342* (DS; R67-L49), *14343* (DS; R67-L48); above Suva, Viti Levu, *Carlquist** (R20191). GHANA. *Morton A4438** (R18084); Legon, *Morton in 1961** ($n = 16$; R16866). INDIA. West Bengal, Garia (Subramanyam, 1971); Indian Botanical Garden, Calcutta (*N. Datta B, C*, 4 plants, meiotic and somatic determinations; Sarkar et al., 1973); Andul, Howrah Distr., *N. Datta A*; Kolaghat, Midnapur Distr., *N. Datta D*. MEXICO. 20 mi S of La Trinitaria, Chiapas, *Breedlove 10039**; 4.5 mi NE of Bochil, Chiapas, *Breedlove 10191**; 5 mi S of Jitotol, Chiapas, *Breedlove 11955* ($n = 16$); 8 mi E of Cintalapa, Chiapas, *Breedlove 10308**; 9 mi SW of Valle Nacional, Oaxaca, *Breedlove 8041**; 3 km N of Valle Nacional, *Stone 1832** (DS); Veracruz, *Romero 77** (DS). MOZAMBIQUE. Malema, Mocambique Dist., *R19635**. NEW CALEDONIA. Tontoroita, *Carlquist in 1962**. NEW HEBRIDES. Espiritu Santo, *Carlquist** (RG65-50). PANAMA. Juan Mina, *Dressler in 1962**. PERU. Nr. Iquitos, *Mathias 3533** (LA, RSA, R18098; $n = 16$, R62036), *3953**, *Dressler** (R20235), *Dressler** (R20183); Muyuy, *Dressler** (R20236). RHODESIA. *Methuen 297** (PRE; R65-192). SAMOA. Saleimoa to Matauta, *Carlquist** (R20669). SIERRA LEONE. *Morton SL1217** (K; R20189). SOUTH AFRICA. Ca. 52 mi W of Louis Trichardt, Transvaal, *Schleiben 7478** (G; R16620). TANZANIA. Mpanda Dist., *Harley 9449** (K; R in 1963). THAILAND. Chiangmai, *Sorensen et al. 5328** (C), *5329* (C). TOGO. Nr. Defale, *Morton A4438** ($n = 16$; R62018). TRINIDAD.

TABLE 2. Continued.

Aripo Savanna, *Jermy* 3183* (BM), 3187* (BM), *H. G. Baker in 1962** (R20269). UNITED STATES. Florida: Prairie Lake, *Schallert* 16221* ($n = 16$; S; R16619); Broward Co., *Sternberg in 1974** (2 collections); Clay Co., R18687 (see below); Collier Co., R18670 ($n = 16$), *Munz & Gregory* 23475 ($n = 16$; RSA; Gregory & Klein, 1960, as *Jussiaea suffruticosa* var. *ligustrifolia*); Highlands Co., R18682 ($n = 16$); Hillsborough Co., R18646 ($n = 16$), R18647 ($n = 16$). Hawaii: Oahu, *Gillett in 1964** (DS). Mississippi: Jackson Co., R18582 ($n = 16$). VENEZUELA. Nr. Samariapo, Amazonas, *Gentry* 14568*, 14608*; Rancho Grande, *Medina in 1964** (R65-187); Caucagua, *Medina** (R20672). ZAÏRE. Nr. Kinzao Vuete, *Compère* 256 (BR; R16669).

Ludwigia octovalvis. Plants with $n = 24$.

AUSTRALIA. Northern Territory, *Nelson* 287* (DS). CHINA. Taichung Co., Taiwan, *De Vol et al.* 433* (R20270), *Chuang & Lin* TIC4780 ($n = 24$; Chuang et al., 1962), *Chuang* TIC3905 ($n = 24$; Chuang et al., 1962), Sah-Pai, Taipei Co., Taiwan, *Chuang et al.* 4318* (R18130). DOMINICAN REPUBLIC. Nr. Santiago de los Caballeros, *Jiménez in 1962** (R65-63). INDIA. Bangalore, *Satyanarayana* 74-147* (R74-147); 150 mi S of Waltair, *P.N. Rao** (R18133); Gauhati, *Santapau* 34797* (R19651); S Kamrup, Assam, *Srinivasan* 39183* (R67-L18). JAPAN. Amami-Oshima, Ryukyu Isls., *S. Hatusima** (R20184). MALAYA. Nr. Kuala Lumpur, Selangor, *Kassim** (R67-L21). NEW GUINEA. Wantipi Village, Sepik Dist., *Darbyshire & Hoogland* 8303* (K; R62037); Bulolo, *Jermy in 1964**, Finisterres, *Jermy in 1964** (R65-96); Mengea, 3,600 ft elev., *Jermy in 1964** (R65-98); Butnari to Wonenara, Eastern Highlands, 6,000 ft elev., *Carlquist in 1963** (R65-60); Aitape Subdistrict, Sepik Dist., *Darbyshire & Hoogland* 8303*. SINGAPORE. Botanical Garden, R65-55*. VENEZUELA. Jardín Botánico, Caracas, *Medina in 1964**.

Sect. *Microcarpium*

Ludwigia alata Ell. Plants with $n = 16$.

UNITED STATES. Florida: Collier Co., R18672*; Highlands Co., R18684 ($n = 16$), R18681 ($n = 16$), R17927*.

Ludwigia alata. Plants with $n = 24$.

UNITED STATES. Florida: Wakulla Co., R18608 ($n = 24$). Georgia: Charlton Co., nr. Cravens Hammock, *R in 1974**. South Carolina: Horry Co., R18719 ($n = 24$).

Ludwigia curtisii Chapman (including *L. simpsonii* Chapman and *L. spathulifolia* Small). Plants with $n = 24$.

UNITED STATES. Florida: Collier Co., *Munz & Gregory* 23476 ($n = 24$; Gregory & Klein, 1960); Hillsborough Co., R18649* (also $n = 24$); Martin Co., *Munz & Gregory* 23481 (RSA; Gregory & Klein, 1960, as *L. simpsonii*); Sarasota Co., R18640 ($n = 24$).

Ludwigia curtisii. Plants with $n = 32$.

UNITED STATES. Florida: Dade Co., *Godfrey* 63396*; Monroe Co., *Godfrey* 63519*; Sarasota Co., R18662*.

Ludwigia glandulosa Walt. ($n = 16$).

UNITED STATES. Alabama: Macon Co., R18562 ($n = 16$). Arkansas: *Demaree* 46645* (R65-42). Florida: Jefferson Co., R18617 ($n = 16$); Leon Co., *Godfrey** ($n = 16$; Gregory & Klein, 1960); Madison Co., R18628 ($n = 16$). Louisiana: St. Tammany Parish, R18577 ($n = 16$); Tammany Parish, R18576 ($n = 16$). Mississippi: Jones Co., R18569 ($n = 16$). Texas: Fort Bend Co., R19398 ($n = 16$), R19405 ($n = 16$); Liberty Co., R19427 ($n = 16$).

Ludwigia linearis Walt. ($n = 8$).

UNITED STATES. Alabama: Baldwin Co., R18590 ($n = 8$). Arkansas: *Demaree* 46998* (R65-43). Florida: Madison Co., R18627 ($n = 8$). Louisiana: St. Tammany Parish, R18579 ($n = 8$). Mississippi: Jackson Co., R18585 ($n = 8$). North Carolina: Cumberland Co., *Lloyd* 1026 ($n = 8$); Johnston Co., *Lloyd* 1121 ($n = 8$). South Carolina: Horry Co., R18721 ($n = 8$).

Ludwigia linifolia Poir. ($n = 8$).

UNITED STATES. Florida: Okaloosa Co., R18593 ($n = 8$). Mississippi: Hancock Co., R18581 ($n = 8$); Jackson Co., *Demaree* 37879* (Kurabayashi et al., 1962; also $n = 8$; Gregory & Klein, 1960).

Ludwigia microcarpa Michx. ($n = 8$).

UNITED STATES. Florida: Clay Co., R18692 ($n = 8$, also in progeny); Hillsborough Co., R18641 ($n = 8$); Wakulla Co., R18601 ($n = 8$), R18610 ($n = 8$).

TABLE 2. Continued.

Ludwigia pilosa Walt. ($n = 16$).

UNITED STATES. Florida: Clay Co., R19690 ($n = 16$); Highlands Co., R18683 ($n = 16$); Leon Co., Kral in 1963* (R65-44); Madison Co., R18625 ($n = 16$); Walton Co., R18594 ($n = 16$). Georgia: Camden Co., R18701 ($n = 16$). Mississippi: Hancock Co., R18580 ($n = 16$); Jackson Co., R18583 ($n = 16$); Jones Co., R18568 ($n = 16$). South Carolina: Colleton Co., R18717 ($n = 16$; see below); Jasper Co., R18712 ($n = 16$).

Ludwigia polycarpa Short & Peter ($n = 16$).

UNITED STATES. Massachusetts: Middlesex Co., R16514 ($n = 16$). Michigan: Washtenaw Co., R16523 ($n = 16$).

Ludwigia sphaerocarpa Ell. ($n = 16$).

UNITED STATES. Without definite locality, Monoson 55* (RSA; Gregory & Klein, 1960). Florida: Clay Co., R18680 ($n = 16$; intermediate to *L. pilosa*); Columbia Co., R18634 ($n = 16$); Madison Co., R18626 ($n = 16$), R18630 ($n = 16$); Taylor Co., R18620 ($n = 16$). Indiana: Starke Co., R16525 ($n = 16$; = "var. *deamii* Fern. & Grisc."). Massachusetts: Plymouth Co., R16516 ($n = 16$). South Carolina: Beaufort Co., R18716 ($n = 16$; intermediate to *L. pilosa*); Colleton Co., R18718 ($n = 16$).

Ludwigia suffruticosa Walt. Plants with $n = 16$.

UNITED STATES. Florida: Glades Co., R18678*; Lake Co., R18637 ($n = 16$); Leon Co., R18585 ($n = 16$); Polk Co., Lakela 24806* (R19704); Taylor Co., R18619 ($n = 16$).

Ludwigia suffruticosa. Plant with $n = 24$.

UNITED STATES. Florida: Hillsborough Co., R18651 ($n = 24$).

Sect. *Miquelia*

Ludwigia ovalis Miq. ($n = 16$).

JAPAN. Kyushu: Prov. Satuma, S. Hatusima 26593* ($n = 16$; R18090), in 1966* (R67-L1).

Sect. *Nematopyxis*

Ludwigia prostrata Roxb. ($n = 8$).

INDIA. Dehra Dun, P.C. Pant 38535*; Lachmansidh, Dehra Dun, M.A. Rau* (BSI); Bihar, Champaran, Gobardhana, Shetty 342 ($n = 8$; Shetty & Subramanyam, 1971).

Sect. *Nipponia*

Ludwigia epilobioides Maxim. subsp. *epilobioides* ($n = 24$).

CHINA. Taipeh, J.M. Chao 1100* ($n = 24$; R18126). JAPAN. Honshu: Chiba Pref., R18093* ($n = 24$); Kyoto, H. Hara in 1961* ($n = 24$; R18082). Kyushu: Kagoshima, S. Hatusima* ($n = 24$; R18086).

Ludwigia epilobioides subsp. *greatrexii* (H. Lév.) Raven ($n = 24$).

JAPAN. Honshu: Chiba Pref., H. Hisauchi in 1961* ($n = 24$). Kyushu: Osumi Pref., S. Sako in 1961* (R18083).

Sect. *Oligospermum*

Ludwigia adscendens (L.) Hara subsp. *adscendens* ($n = 16$).

CHINA. Hong Kong* (no voucher, living plants sent by C. DeVol). INDIA. Without definite locality (M. Jash in Sharma & Sharma, 1966, as *Jussiaea repens*); West Bengal (2 localities; N. Datta in litt.). THAILAND. SE of Chiangmai, Sørensen et al. 5018* (C).

Ludwigia adscendens subsp. *diffusa* (Forsk.) Raven [*L. stolonifera* (Guill. & Perr.) Raven] ($n = 16$).

GHANA. Nungua Dam, Morton A4139* ($n = 16$; R16670); Accra Plains, Morton A4139*. IRAQ. Amara Marshes, Al-Rawi* (R19656). KENYA. Leita Dist., Hocombe 1506* ($n = 16$; R16771). RHODESIA. Beitbudge Dist., Drummond 6119* (K).

Ludwigia helminthorrhiza (Mart.) Hara ($n = 8$).

PANAMA. Gamboa, Canal Zone, Dressler* (R19653).

Ludwigia hookeri (Mich.) Hara ($n = 8$).

BRAZIL. Florianópolis, Santa Catarina, Sehnem 7* ($n = 8$).

Ludwigia peploides (H.B.K.) Raven subsp. *glabrescens* (O. Kuntze) Raven. Populations with $n = 8$.

TABLE 2. Continued.

FRANCE. Vias, Hérault, *L. Berner** (R20133). MEXICO. Chiapas: San Cristóbal las Casas, *Breedlove* 7163*. Chihuahua: 14 mi W of Matachic, *Wiens* 3462 ($n = 8$). UNITED STATES. Arkansas: Clark Co., *Demaree* 48954* (R19655). Texas: Fort Bend Co., R19404 ($n = 8$); Llano Co., R19323 ($n = 8$); Presidio Co., *Gregory* 224 ($n = 8$; Gregory & Klein, 1960).

Ludwigia peploides subsp. *glabrescens*. Populations with $n = 16$.

UNITED STATES. Mississippi: Jones Co., R18573 ($n = 16$).

Ludwigia peploides subsp. *montevidensis* (Spreng.) Raven ($n = 8$).

AUSTRALIA. South Australia, R18094*. CHILE. Nr. Farellones Ski Resort above Santiago, *Wiens** (R67-L10). UNITED STATES. California: Stanislaus Co., R16610 ($n = 8$; Raven, 1963b).

Ludwigia peploides subsp. *peploides* ($n = 8$).

UNITED STATES. California: Rancho Santa Ana, Los Angeles Co. ($n = 8$; no voucher; Gregory & Klein, 1960); San Bernardino Co., *R in 1961** (RSA).

Ludwigia peploides subsp. *stipulacea* (Ohwi) Raven ($n = 8$).

JAPAN. Without definite locality (Sinotô, 1928). Honshu: Miura City, Kanagawa Pref., *S. Ohtani* s.n.

Ludwigia uruguayensis (Camb.) Hara. Populations with $n = 24$.

BRAZIL. Rio Grande do Sul, *Sehnem** (RG62090). UNITED STATES. Florida: Bradford Co., R18693 ($n = 24$, multivalents common). Texas: Chambers Co., R19423 ($n = 24$, multivalents common).

Ludwigia uruguayensis. Population with $n = 48$.

UNITED STATES. North Carolina: New Hanover Co., *Gregory* 531 ($n = 48$, multivalents common).

Ludwigia uruguayensis. Populations with $n = 40$.

COSTA RICA. Just above Cartago on road to Irazú, R22038 ($n = 40$). FRANCE. Unvouchered material from southern France, sent as living plants*. UNITED STATES. California: Los Angeles Co., Botanical Garden, University of California (no voucher; determined by M. Kurabayashi); Tiburon, Marin Co., R16563 ($n = 40$; multivalents common); Stanford, Santa Clara Co., R16590 ($n = 40$; multivalents common).

Sect. *Prieurea*

Ludwigia senegalensis (DC.) Troch. (*L. pulvinaris* Gilg) ($n = 8$).

SIERRA LEONE. Road from Morea Junction to Fintonia Natl. Park, *Morton* SL586*. ZAMBIA. Kalabo, *Fanshawe* F8060* (R18725).

Sect. *Seminuda*

Ludwigia affinis (DC.) Hara. Populations with $n = 32$.

BRAZIL. Terr. Amapá, Rio Araguari, *Pires et al.* 51342* (NY). PERU. Nr. Iquitos, Dept. Loreto, *Dressler in 1964** (R20675).

Ludwigia affinis. Populations with $n = 40$.

SIERRA LEONE. *Morton* SL848*. VENEZUELA. Caucagua, *Medina in 1964**.

Ludwigia africana (Brenan) Hara ($n = 24$).

ZAÏRE. Djombi-Djungu, *Déville* 512* (BR; R16772, R18095).

Ludwigia leptocarpa (Nutt.) Hara. Populations with $n = 16$.

ECUADOR. Galápagos Islands, *Wiggins* 18790 (DS). PANAMA. Barro Colorado I., *R. King** (RG63028). UNITED STATES. Alabama: Baldwin Co., R18587 ($n = 16$). Arkansas: *Demaree* 51267* (DS). Florida: Clay Co., R18688 ($n = 16$); Taylor Co., R18621 ($n = 16$); Walton Co., *Godfrey* 57651* ($n = 16$; RSA; Gregory & Klein, 1960). Georgia: Pierce Co., R18085* ($n = 16$), *Ahles in 1962**. Illinois: Massac Co., *Evers* 82276* (RG65-79). Louisiana: St. Tammany Parish, R18578 ($n = 16$). Mississippi: Lamar Co., R18575 ($n = 16$).

Ludwigia leptocarpa. Populations with $n = 24$.

GHANA. Brinsu, *Hall* 2864 (R65-186); nr. Weija. *Morton** ($n = 24$; DS; R16668).

^a An asterisk indicates progeny grown in the experimental garden from the collection indicated.

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